NOTES ON PROSOBRANCHIATA.

No. iii.—The Neanic Shell of *Melo diadema*, Lamk., and the Definition of the Nepionic Stage in the Gasteropod Mollusc.

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A. Neanic Shell of *Melo diadema*, Lamk.
   (1) Description of shell and mass of egg-capsules.
   (2) The succession of the columellar folds.

B. Definition of the Nepionic Stage in the Gasteropod Mollusc.
   (1) A comparison of Molluscan stages of development with those of the *Lepidoptera*.
   (2) Three types of transition from Embryonic to Neanic shell-structure, and suggestions as to their explanation and significance.
   (3) Conclusions arrived at.

C. A short list of works in which protoconchs are described, or in which the auxological terms are discussed.

A. Neanic Shell of *Melo diadema*, Lamarck.

Description of shell and mass of egg-capsules.—The following remarks are to some extent inspired by a short note by Mr. B. B. Woodward* on the nepionic shells of *M. indicus*, Gmel., in a recent part of the Proceedings of the Malacological Society. His note led me to examine similar specimens of *M. diadema*, Lamk., and apices of many other *Volutes;* and I have arrived at the conclusion that it is probable that the formation of adult structure within the egg-capsule is common to many of the Volutidæ, if not all.

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* Woodward, Proc. Malac. Soc. Lond., v., No. 4, 1803, p. 260.

The capsule mass is oval in transverse and longitudinal section; its dimensions are 155 × 60 × 50 millimetres, and was apparently attached by one end; it contains about eighty individuals, all with their apices turned outward and their anterior canals towards the centre.

As far as may be judged from young specimens of *M. indicus* at my disposal, the shell of *M. diadema* when it bursts the capsule is similar to those on which Mr. Woodward founded his remarks.

Specimens which entirely fill their respective capsules consist of a protoconch of three and one-half whorls, and one-half whorl of adult structure. Such a specimen measures 28 mm. in length and 16 in breadth, the length of the aperture being 21 mm. The crown of the spire is flat, the nucleus being slightly depressed. The protoconch is very faintly defined from the succeeding structure by the possession of obsolescent revolving liræ, and a slight and somewhat abrupt thickening of the shell. It is probable that this protoconch was cast inside a horny original, which was discarded at an earlier stage than I have been able to study.

Dr. Dall* was able to demonstrate that the protoconch of *Scaphella magellanica*, Sby., was cast inside a horny original.

This calcareous cast of a primitive horny shell, when it has been deposited subsequent to the veliger, is in the following pages designated the *pseudoprotoconch*, in contradistinction to the true protoconch, which was secreted previous to or during the veliger. Many true protoconchs are, however, calcareous, as for example those of the various species of *Triphora*.

The succession of the columellar folds.—Before proceeding to discuss the definition of the nepionic stage, it will be in order to draw attention to the sequence of the acquisition of the columellar plaits. This is of particular interest, as being in perfect conformity with Dr. Dall's† phylogenetic scheme of their origin, viz.:—The first to appear is the anterior, and the last the posterior, this last being subsequently aborted. The anterior, which in

* Dall, Bull. Mus. Comp. Zool. Harvard, xviii., 1889, p. 452.

† Dall, Wagner F. Inst. Sci. iii., pt. 1, 1889, p. 58 *et seq.*

Melo is merely an emphasis of the columellar edge, appears on the protoconch (pseudoprotoconch ?) when only two whorls have been formed; the third follows so soon after the second that they may be said to arise simultaneously, on the completion of two and one-half whorls; the fourth arises a quarter of a whorl later. The last gradually degenerates after the formation of five whorls, and has generally disappeared by the time six and one-half whorls are completed, though it may occasionally persist throughout the ephebic stages.

For reasons stated in the next section of this paper, the structure which follows the protoconch (pseudoprotoconch ?) in *M. diadema* is to be regarded as neanic, and it is interesting to find that though there is no external differentiation, the neanic stages are clearly defined, by the retention of the fourth fold.

The order of succession of the plaits in *M. æthiopica*, Linn., is doubtless on the same lines as in the above species; there are generally only three plaits present in adult specimens, but one example of eight whorls had all four plaits fully developed.

The position of this fourth plait is always on the posterior boundary of the sinūs left in the track of the anterior canal. It is possible that the ridge sometimes present at the posterior boundary of these sinūs is the cause of the occasional retention of the plait.

B. Definition of the Nepionic Stage in the Gasteropod Mollusc.

Recent papers dealing with protoconchs provide a fairly wide range of facts, which may be taken as the basis of speculation on this interesting minor problem.

The nepionic (brephic or silphologic) stage was defined by Buckman & Bather* as that immediately succeeding the embryonic stages, and during which no specific characters make their appearance. The next, neanic (nealogic) stage they defined as that during which specific characters and all other morphological features present in the adult, appear and undergo development.

* No. 15 appended bibliography.

Both Harris and Jackson (7, 16) conclude that specific characters make their appearance in the nepionic stage. This conclusion was, however, it is here contended, due to the misapplication of the terms, the stage in which they recognised these specific characters being the neanic.

That the nepionic stage, as defined above, exists throughout whole orders no student of Ontogeny will deny. To cite the example used later, the short stage during which the Lepidopterous larva changes into the pupa cannot be regarded as embryonic, neither can it be regarded as neanic, for certainly no specific characters appear until the formation of the pupa, which must therefore be regarded as neanic. Specific characters *almost invariably* make their appearance in what these authors call the nepionic (brephic) stage of the Gasteropoda. From an extended study of *Lotorium* growth-stages, I find that it is possible to identify almost any species of that genus from one-half whorl of post-embryonic structure. On the other hand, it is often possible to recognise a species from purely embryonic characters, *e.g.*, *Triphora*. But what is desired here is to point out that there *are* whole orders in which the nepionic stage as above defined is *easily* recognisable, whilst with the Gasteropoda, in that stage which has hitherto been designated nepionic (brephic), specific characters are generally recognisable. That is to say, the various species of a given genus are already differentiated one from another in that stage. The explanation lies in the fact that in this class (Gasteropoda) the true nepionic stage is a very transitory one, and leaves, in most cases, no conchylaceous record. If this be not recognised, the auxological terms will have one set of meanings for Mollusca and another for other organisms.

Comparison of Molluscan stages of development with those of the Lepidoptera.—That the various stages of development may be the better understood, it will be well to apply the auxological terms to the Lepidoptera; organisms in which the primary divisions are emphasised and easily definable, and then to homologise the molluscan stages with them.

The embryonic stage closes with the larva, which is the phylembryo. The pupa has acquired the adult organs and must therefore be regarded as the neanic stage, since it is that in which the adult characters first appear. The nepionic stage must consequently be, in a silkworm for example, that during which it spins its cocoon and becomes metamorphosed into the pupa. The imago is the ephebic stage.

Homologising the molluscan stages with the above, the veliger is the phylembryo. The nepionic stage is so contracted as to be generally unrecognisable and (probably) non-existent conchylaceously. It is however, here as in the *Lepidoptera*, that stage during which the larval organs degenerate and disappear. The neanic stage during which the adult characters appear and undergo development is generally so graduated into the succeeding ephebic stage that only in a few instances can its ultimate limit be defined. Early adult shell-structure is, however, doubtless neanic, as is also the pseudoprotoconch.

Three types of transition from embryonic to neanic shell-structure, and suggestions as to their explanation and significance. —The investigations of the writers mentioned in the appended bibliography have brought to light three very distinct types of transition from embryonic to neanic shell-structure, viz. :—

(1) Those in which the embryonic is faintly, if at all, defined from subsequent structure. Examples are *Melo indicus*, *Lotorium abbotti*, Tenison-Woods, and most species of *Triphora*.

(2) Those in which there is an abrupt change from embryonic to subsequent structure. This occurs in all the recent species of *Lotorium*.

(3) Those in which a varix is thrown up at the conclusion of the protoconch before the neanic structure is initiated. According to F. C. Baker* most of the Murices fall into this category.

Remembering that the primitive shell-gland is distinct from the area which secretes the adult or, as Lankester† aptly terms

* Baker, Proc. Acad. Nat. Sci. Philad., 1890, p. 66 *et seq.*

† Lankester, Ency. Brit. edit. 9, xvi., p. 639, 1885.

it, secondary shell, the following suggestions are advanced in explanation of the above types of transition.

In the first type it seems probable that, parallel with the gradual cessation of functional activity on the part of the primitive shell-gland, there was a gradual assumption of secretive activity on the part of the epithelial cells of the mantle and visceral hump. In *Melo* the acceleration of development which the formation of neanic structure within the egg-capsule presents, points to a correspondingly transitory nepionic stage, consequently there is only a slight defining line. It is evident from the weight and size of the neanic shell described above that, as in *Neritina* and *Onchidium*, the veliger stage of *M. diadema* is passed within the egg. In *Triphora*, on the other hand, there is an extreme protraction of the veliger stage; it has been obtained in mid-ocean with several adult whorls already formed. In this genus the true embryonic shell or protoconch is calcareous. Doubtless the original cap of the smooth nucleus was horny; we are nevertheless not dealing with a pseudoprotoconch, for whilst still a veliger or phylembryo the organism had acquired the ability to secrete a calcareous shell. The explanation given at the beginning of this paragraph still applies, but in this instance the transference of functional activity from the primary to the secondary shell-secreting area took place some time prior to the nepionic stage. The protracted retention of the velum here allows a much greater development of the other organs, so that the mantle edge assumes its adult form and secretes shell-structure which, although genetically embryonic, is morphologically adult. The other organs being well advanced in development, the nepionic stage is concerned only with the degeneration of the velum, in these instances also it will be very condensed. From these remarks it may be reasonably expected that this type of transition will prove to be correlated with an extremely condensed nepionic stage.

The metamorphosis of organs just mentioned appears at first sight to be nepionic, but as long as the organism retains the velum in full development it is to be regarded as a phylembryo;

if this be not admitted, it becomes impossible to define the embryonic stages.

Taking as my base the genus *Lotorium*, in examining the second type of transition I am presented with the following facts. The true protoconch is horny and contains practically no calcareous matter. During the formation of at least part of this, the organism is a free-swimming veliger; the same applies to *Gyrineum australasia*, Perry. The next stage I am acquainted with is that in which a little less than half a whorl of neanic structure has been added. The protoconch has now deposited within it distinct traces of the pseudoprotoconch in the form of an extremely thin layer of calcareous lining, the neanic structure being much thicker and exhibiting the adult sculpture in miniature. The mollusc itself is sedentary and has lost all traces of the velum. The abrupt transition from one structure to the other may be explained by the sudden functional activity of the secondary shell-secreting area. It is probable that during the nepionic stage, which was slightly protracted, there was a complete cessation of shell-growth, and that the primitive gland had ceased its function before the secondary shell was initiated.

As an example of the third class of transition, perhaps the rarest and most interesting, *Murex denudata*, Perry, exhibits the following characters:—A stout calcareous protoconch longitudinally sculptured, followed by a prominent varix, the succeeding neanic structure exhibiting, in miniature, all the adult characters. The sculpture of the protoconch is such as to prove conclusively that it was not cast inside a horny mould and is therefore a true protoconch. *The embryo thus had the ability to secrete a calcareous shell.* It seems reasonable to suppose that during the nepionic stage (during which there must generally be a longer or shorter pause in the growth of the mollusc) the secretion of shell was carried on by the free edge of the mantle. Granted this, the varix may be looked upon as the conchylaceous record of the nepionic stage.

Conclusions arrived at.—The perfection of internal organs during the veliger stage, postulated above for *Triphora*, has been

demonstrated in other Mollusca;* we are therefore led to the following definition of the nepionic stage in the Gasteropod mollusc :—*That stage during which the velum undergoes degeneration and disappears.*

And a theory I advanced some time ago is still maintained, namely :—*Where no varix is thrown up at the conclusion of the embryonic shell, no conchylaceous record of the nepionic stage has been left by the mollusc.*

A more explicit definition of the nepionic stage than Buckman and Bather's would be :—That stage during which the larval organs become aborted. The above definition of this stage in the Gasteropod Mollusc is, therefore, only a specific form of the general definition.

It has been suggested to me in the course of discussion that the pseudoprotoconch is the homologue of the above varix. This suggestion is a good one, and it is likely that some pseudoprotoconchs are nepionic, but it does not apply to those of *Lotorium*, as shown by the extreme thinness of the calcareous lining of the young specimen described above.

C. A short list of works in which Protoconchs are described, or in which the auxological terms are discussed.

1.—Baker, F. C.—"On the Modifications of the Apex in *Murex*." Proc. Acad. Nat. Sci. Philadelphia, 1890, p. 66 *et seq.*

2.———"Descriptions of New Species of *Murices*, with remarks on the Apices of certain forms." Proc. Rochester Acad. Sci. i , 1891, p. 129 *et seq.*

3.———"Modification of the Apex in Gasteropod Mollusks." Ann. New York Acad. Sci. ix., 1897, p. 685 *et seq.*

4.—Dall, W. H.—"Blake Mollusca." Pt. ii. Bull. Mus. Comp. Zool. Harvard Coll. xviii., 1898.

5.———"Tertiary Mollusca of Florida." Trans. Wagner Free Inst. Sci. iii., pts. 1 and 2, 1890 and 1892.

* Fide Korschelt & Heider, Text Book of Emb. Invert. M. F. Woodward's edit., iv., p. 133.

6.—Grabau, A. W.—"Studies of Gasteropoda." American Naturalist, xxxvi., No. 432, 1892, p. 917 *et seq.*

7.—Harris, G. F.—Brit. Mus. Cat. Tertiary Mollusca. Pt. i. Australasia, 1897.

8.—Hedley, C.—*Triforis* in "The Mollusca of Funafuti." Mem. Australian Mus. iii., Pt. 7, 1899, pp. 439-448.

9.———"The Triphoridæ of New South Wales" in "Studies on Australian Mollusca, Pt. 7." Proc. Linn. Soc. N.S. Wales, xxvii. Pt. 4, p. 606 *et seq.*

10.—Kesteven, H. Leighton.—"The Systematic Position of *Purpura tritoniformis*, of Blainville." Proc. Linn. Soc. N.S. Wales, xxvi. Pt. 4, 1902, p. 533 *et seq.*

11.———"The Protoconchs of Certain Port Jackson Gasteropods." *Loc. cit.* p. 709 *et seq.*

12.———"A Note on two species of *Astralium* from Port Jackson." *Op. cit.* xxvii. Pt. 1, 1902, p. 2 *et seq.*

13.———"Notes on *Prosobranchiata*. No. 1. *Lotorium*." *Op. cit.* Pt. 3, p. 443 *et seq.*

14.—Watson, R. B.—"Gasteropoda." Challenger Reports, Zoology, xv., 1886.

The above list might have been lengthened by enumerating papers in which one or two apices are described incidentally, in specific definitions, but it contains the most important works, and their consultation will give references to many others. Several of the text-books contain interesting remarks on the subject and are well worth consulting. Tate's papers on the "Gasteropods of the Older Tertiaries of Australia" give several short descriptions and a few figures of apices. The following are the works in which the auxological terms have been discussed :—

15.—Buckman, S. S., and Bather, F. A.—"The Terms of Auxology." Zoologischer Anzeiger, No. 405, 1892, p. 421; No. 406, p. 429.

16.—Hyatt, A.—"Values in Classification of the Stages of Growth and Decline, with Propositions for a new Nomenclature." Proc. Boston Soc. Nat. Hist. xxiii. 1888, pp. 396-408.

17.———"Genesis of The Arietidæ." Mem. Mus. Comp. Zool. Harvard Coll. xvi. No. 3, 1889.

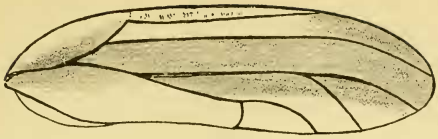
18.—Hyatt, A.—"The Terms of 'Bioplastology,' 'Ontogeny.'" Zoologischer Anzeiger No. 427, 1893, p. 325.

19.—Jackson.—"Phylogeny of the Pelecypoda." Memoirs Boston Soc. Nat. Hist. iv. No. 8, 1890, p. 290.

Postscript.—After this paper was read Mr. C. Hedley drew my attention to a paper by Dr. Willey,* "On the Nepionic Shell of the Recent *Nautilus*," in which the author regards the date of hatching as the date of the conclusion of the nepionic stage. He says :—"Thus the nepionic shell of the ('terrestrial Gasteropod') molluscs is that portion of the true shell (as opposed to the embryonic shell), which develops within the egg." This, I venture to suggest, is a misinterpretation of the term. If we accept, as we must, Dr. Jackson's definition of the Molluscan phylembryo as the veliger and last embryonic stage; and if the velum becomes aborted within the egg, however quickly; then that stage during which this "larval organ" is aborted, must, as in other cases, be recognised. Thus, such a mollusc, terrestrial or otherwise, has already entered upon the neanic stage before leaving the egg. Some Anuran Amphibia are hatched in the adult form, but we do not regard them as tadpoles, because most of the Anura are hatched as tadpoles. We cannot say what stage of development *Nautilus* is hatched in, so that the shells discussed by Dr. Willey in the paper referred to may be rightly termed "nepionic"; on the other hand they might equally well be neanic *(September 25th, 1903)*.

* Willey, Quart. Journ. Microscop. Sci., xxxix., pp. 222-230, 1897.

[Printed off September 30th, 1903.]



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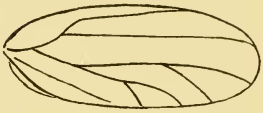

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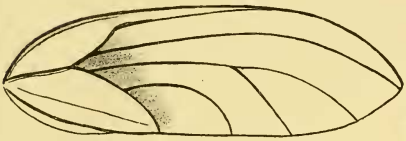

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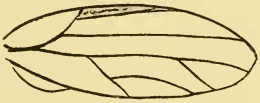

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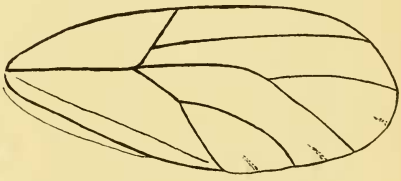

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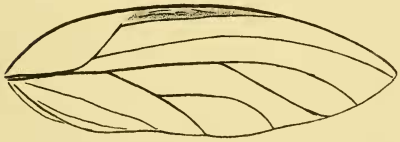

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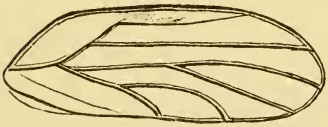

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AUSTRALIAN PSYLLIDAE.